THE ACTINOPTERYGIAN FISH *PROHALECITES* FROM THE TRIASSIC OF NORTHERN ITALY

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ABSTRACT. The bony fish *Prohalecites* is redescribed from new well-preserved material from the locality of Ca' del Frate (northern Italy), dated close to the Ladinian–Carnian boundary. A few poorly preserved specimens from the type locality, Perledo (Ladinian), have also been restudied. The specimens represent several ontogenetic stages as evidenced by vertebral column development, and it is concluded that in structure *Prohalecites* is intermediate between the Parasemionotidae and *Dapedium* plus the Pholidophoridae, being closer to the last two. In fact *Prohalecites*, though similar to some of the Parasemionotidae in the dermal skull covering, has a splint-like quadratojugal, similar in shape and position to that of the Pholidophoridae, but not fused to the quadrate (as is the case for *Dapedium*), and ural neural arches approaching the uroneural condition of the Pholidophoridae.

NEW finds in the Kalkschieferzone (top member of the Meride Kalk) near Ca' del Frate (Viggiú, Varese) offer an opportunity for a revision of the genus *Prohalecites* Deecke 1889, so far known only from the Ladinian of Perledo (Como). New stratigraphical data (Gaetani *et al.*, in prep.) point to an uppermost Ladinian to lowermost Carnian age, which is somewhat older than previously thought (Tintori *et al.* 1985). The Kalkschieferzone is characterized by more or less marly limestone, often in thin laminated layers. The depositional environment was marine, but probably influenced by continental areas; this hypothesis is supported by the presence of the conchostracan crustacean *Palaeolimnadia*, a fresh-water dweller (Tintori, in press). The body parts and eggs of these organisms are often well preserved because of the total lack of oxygen in the fossilization environment.

Prohalecites has not been found in the Besano–Monte San Giorgio Scisti Ittiolitici di Besano (Grenzbitumenzone) (Tintori and Renesto 1983), which includes the Anisian–Ladinian boundary. Unfortunately most of the original material used by Bellotti (1857), Deecke (1889) and De Alessandri (1910) has been lost or destroyed during the last World War. Furthermore, no material has been collected in the Calcare di Perledo–Varenna (Calcare di Perledo in Tintori *et al.* 1985) for at least fifty years since the cessation of quarrying.

MATERIAL

So far only the topmost part of the Ca' del Frate horizon (now thought to be the basal part of the Kalkschieferzone of the Meride Kalk) has been extensively studied. Most of the *Prohalecites* specimens come from only two bedding planes. Those from the lower, paler bedding planes (a few cm below the upper darker one) are generally smaller. This does not represent a taxonomic difference but rather a mass mortality event which affected a school of juvenile specimens, perhaps in a different season (summer?) from the later event which caused the mortality at the upper level. A great number of *Palaeolimnadia* has been found on a bedding plane similar to the upper one, and it is hypothesized that this upper deposition may have occurred during the rainy season (autumn/winter?), the Conchostraca having been transported into the Ca' del Frate marine environment by river flooding from a nearby island (Tintori, in press).

On both surfaces the small fishes occur at an average of about one in 100 cm^2 and, even though most of them show more or less the same orientation, a few specimens are randomly scattered. The

alignment may be due to a weak bottom current, but this seems unlikely since the fishes are always complete and their bones articulated. Most of the larger fishes, as well as some of the smaller, have the skull crushed dorso-ventrally, showing either the skull-roof or the gular region with the jaws and sometimes part of the snout. This kind of preservation is related to the very wide head of *Prohalecites*. The body is usually preserved in lateral view, but occasionally it is irregularly twisted. Thus the sea bottom must have had very low energy currents and a very high sedimentary rate to cause rapid burial of the dead fishes by the calcareous mud. Anoxic conditions were also present (see above).

SYSTEMATIC PALAEONTOLOGY

Subclass ACTINOPTERYGII Cope 1871
Infraclass NEOPTERYGII Regan 1923
Genus PROHALECITES Deecke, 1889
PROHALECITES PORROI (Bellotti, 1957)

Plate 1; Text-figures 1–9

1857	*Pholidophorus porro* Bellotti, p. 430.
1853–1860	*Pholidophorus porro* Bellotti; Costa, p. 65, pl. 5, fig. 9–9b.
1866	*Pholidophorus porro* Bellotti; Kner, p. 185.
1889	*Prohalecites porro* (Bellotti); Deecke, p. 125, pl. 7, figs. 5–7.
1895	*Prohalecites* (?) *porro* (Bellotti); Woodward, p. 489.
1910	*Prohalecites porroi* (Bellotti); De Alessandri, p. 137, pl. 9, figs. 4–5.

Diagnosis (emended). Very small naked fish. Rostral followed by broad contiguous nasals. Maxilla short, no supramaxilla, quadratojugal splint-like. Preopercular made from two bones, the dorsal one being tube-like. Five infraorbitals. Parietals sometimes fused. Unpaired median extrascapular often present. Vertebral segments about 33 with hemichordacentra. Epineurals and supradorsal present. Vertebral column diplospondylous in the caudal region; unpaired median neural spines; ural–neural arches as primitive uroneurals; ural chordacentra; a few urodermals present.

Type specimens. The original material described by Bellotti (1857) was destroyed during the last World War. However I do not think it necessary to designate a neotype, the species being easily recognizable and the only one in the genus. The following material can be considered as topotypes: eleven specimens of which one is from the Curioni collection in the Museum of the Geological Survey of Italy in Rome (no catalogue number), seven are from the Ruppel collection in the Senckenberg Museum in Frankfurt am Main (SM P1239a,b; P1245-7-8; P1251-4; P1262), one is from the Paläontologisches Institut und Museum der Universität in Zürich (PIMUZ AI-551), and two are from Costa's collection in the Museo di Paleontologia dell'Università di Napoli (MPUN M172-3-4; M174, being the counterpart of M173).

There are no accurate locality data with these specimens, although they are probably from the quarries in the middle to upper part of the Calcare di Perledo–Varenna. The available specimens are small and poorly preserved, some of them being only counterparts. Latex peels have been made, but are uninformative. Nevertheless, the fishes' position is interesting: they are often in lateral view but, as in several Ca' del Frate specimens, the entire skull-roof is visible. No single bone shape is detectable, owing to a peculiar kind of

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EXPLANATION OF PLATE 1

Prohalecites porroi (Bellotti 1857). Scale bars, if not otherwise stated, 10 mm. 1, two specimens (MCSNIO P370/1–2, 38 and 36 mm s.l.) on one of the two major fossiliferous surfaces (the darker one), both dorso-ventrally crushed. 2, mature specimen (MCSNIO P349a, 30 mm s.l., see also text-fig. 7B) with skull in lateral view; note thoracic hemichordacentra and stout paired neural arches as well as pleural ribs articulating with parapophyses. 3, mature specimen (MCSNIO P373/1, 41 mm s.l., see also text-figs. 4A, 7C); note thoracic hemichordacentra with no intercalaries. 4, young specimen (MCSNIO P341/1, 31 mm, see also text-fig. 7A) with small hemichordacentra only in the middle of the caudal region; skull shows inner surfaces of the roofing bones and of the left lower jaw as well as external surface of the right side bones. 5, young specimen (MCSNIO P376, 23 mm s.l.) with no hemichordacentra (scale bar, 5 mm).

PLATE 1
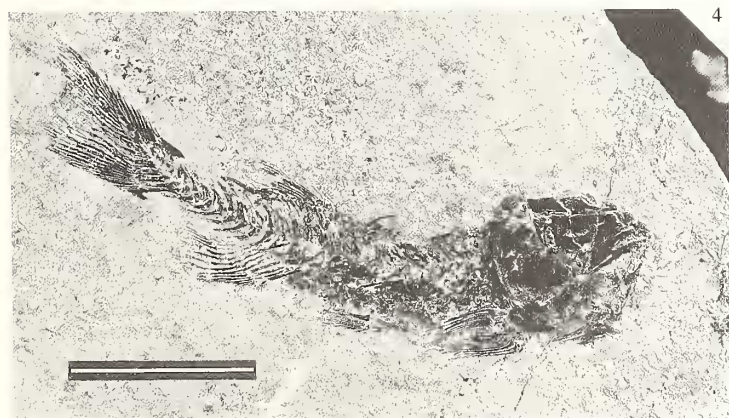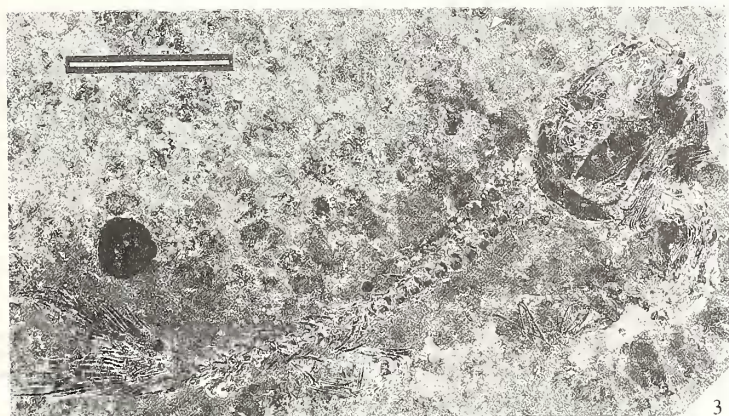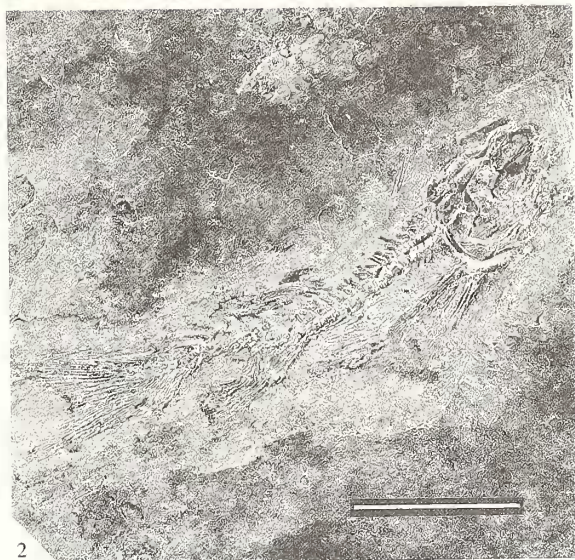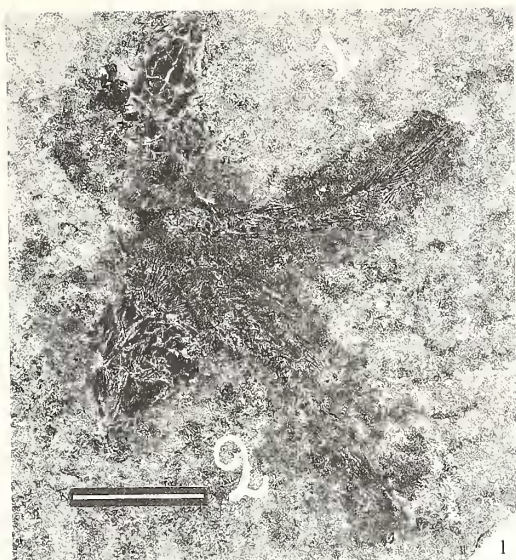
preservation in which the original bone is usually no longer present; only a rough natural mould shows the general shape of the fish.

Other material. The 334 specimens stored in the Museo Civico di Storia Naturale di Induno Olona, Varese (MCSNIO P328 to P416). Three more specimens from Ca' del Frate, but labelled as from Besano, are in the British Museum (Natural History) collection (BMNH P.19471–3; C. Bender Collection, purchased in 1935). The new specimens considered in this paper were prepared mainly with dilute acetic acid, but mechanical techniques were used on occasion. Most of the observations concern a few dozen specimens.

Horizon and locality. The topotypes are from near Perledo (Como, northern Italy), most probably from the upper part of the Calcare di Perledo–Varenna (Scisti di Perledo *auct.*; Upper Ladinian, Middle Triassic). The other material is from the Kalkschieferzone (upper member of the Meride Kalk) near Ca' del Frate (Viggiú, Varese, northern Italy).

DESCRIPTION

Skull and lower jaw

The nasals (text-figs. 2,3) are joined along their whole length; the posterior nostril must have opened on the lateral side of the nasal where a notch is present, while the anterior one presumably opened along the anterior margin. The rostral (text-figs. 2–4) contains the ethmoid commissure and there is a lacuna in the bony cover of the snout where the supraorbital sensory canal may have joined the ethmoid commissure itself. The true position of the antorbital (text-fig. 2) is not clear: it probably touched the corresponding nasal but not the rostral.

The skull roof is very wide in the orbital region and the frontals (text-figs. 2,3) are very broad posteriorly. The parietals (text-figs. 2,3) are sometimes fused, giving rise to a large shield posterior to the frontals. The parietal pit-lines are seen as grooves, lacking the thin ganoine layer which elsewhere covers these bones.

The dermopterotic (text-figs. 2,3) is trapezoidal. The sensory canal branches at about the posterior third to connect with the preopercular sensory canal. In at least one specimen the dermopterotics seem to have fused to the adjoining roofing bones.

The extrascapulars (text-figs. 2,3) are unusual: three to four bones carry the temporal commissure. Between the two lateral bones sometimes there is a third, narrow, unpaired element with two symmetrically arranged pores. Paired median extrascapulars are present in several other specimens.

Posterior to the antorbital and to the postero-lateral corner of the nasal there are three supraorbitals (text-figs. 2,3), the first of which is somewhat larger than the other two. The supraorbitals are followed by the dermosphenotic and the infraorbital series comprising five elements (text-figs. 2,3). The two most dorsal infraorbitals bear up to three denticles on their posterior margins.

Only one suborbital (text-figs. 2,3) the upper, is known with certainty: it completely covers the uppermost part of the preopercular. Traces of a second suborbital have been seen only in MCSNIO P362 from Ca' del Frate and in MPUN M173 from Perledo, but from the configuration of the cheek we can infer that a second suborbital was probably present.

The maxilla (text-figs. 2,4) is about half as long as the lower jaw, ending free below the middle of the orbit. The whole oral margin bears about 20 teeth and it is thickened, especially in the central part. No traces of a supramaxilla have been detected. The teeth are very long and conical: the dentition is remarkably powerful for such a small fish.

The premaxilla (text-figs. 2,4) is triangular: the oral margin bears seven or eight teeth similar to those of the maxilla. A stout nasal process is present lying under the rostral and possibly reaching the nasal. Both the maxilla and the premaxilla are ornamented with flecks of ganoine. The lower jaw (text-figs. 2,4) bears a very high coronoid process. The dentary is the largest bone, with about 20 teeth. The sensory canal ran only in the dentary, probably being free for a short distance between the hind tip of the dentary itself and the ventral preopercular. Dorsal to the angular is the surangular which shows a very small exposed area, much as in *Amia*, and it is seen in only one specimen (MCSNIO P370/3). A notch is present in the lower half of the posterior margin which presumably received the articulatory head of the quadrate. However, it is not clear whether the notch is a true articulatory notch or is like the feature found in the same position in *Amia*. The true articulation pattern is not detectable.

The opercular (text-figs. 2–4) is very broad. The subopercular is subtriangular and the interopercular is small and trapezoidal. All the opercular bones are ornamented with small tile-like ganoine flecks.

The branchiostegal rays (text-figs. 2,4) are at least ten in number, gently decreasing in size forwards. The
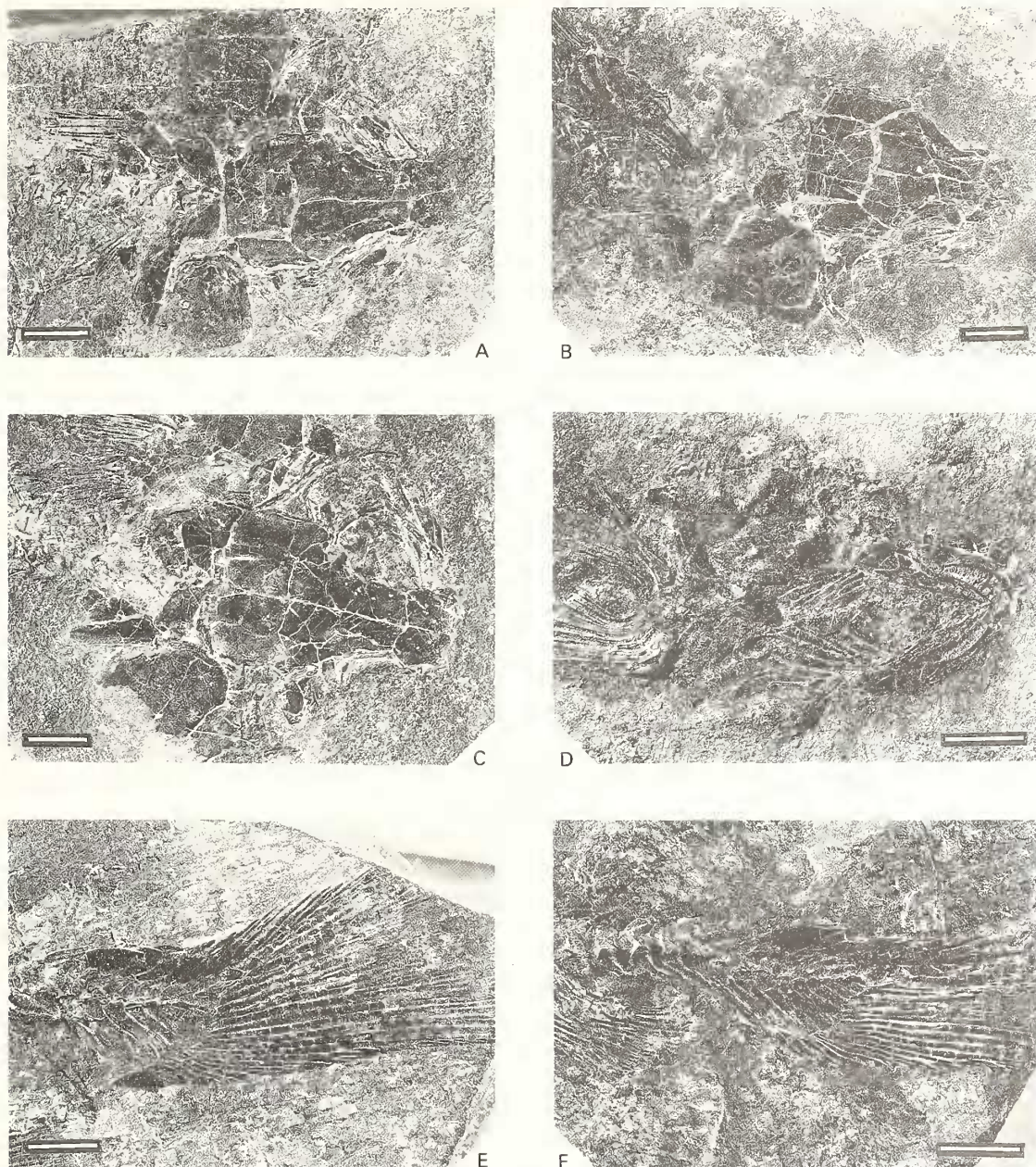
TEXT-FIG. 1. *Prohalecites porroi* (Bellotti 1857). A, head of a 33 mm long specimen (MCSNIO P328/1, see also text-fig. 3B); note the fused parietals and the unpaired median extrascapular. B, head of a 35 mm long specimen (MCSNIO P379) with fused parietals. C, head of a mature fragmentary specimen (MCSNIO P353); note the S-shaped left dorsal preopercular and the two right lateral line scales behind the supracleithrum. D, ventral view of a 35 mm long specimen (MCSNIO P370/3). E, caudal fin of a 30 mm long specimen (MCSNIO P335, see also text-fig. 9B). F, caudal fin of a 33 mm long specimen (MCSNIO P411). Scale bars, 2 mm. Lengths of fishes quoted are standard lengths (s.l.).

TEXT-FIG. 2. *Prohalecites porroi*. Restoration of the skull. A, lateral view; B, dermal skull roof. Length of skull, c. 10 mm.
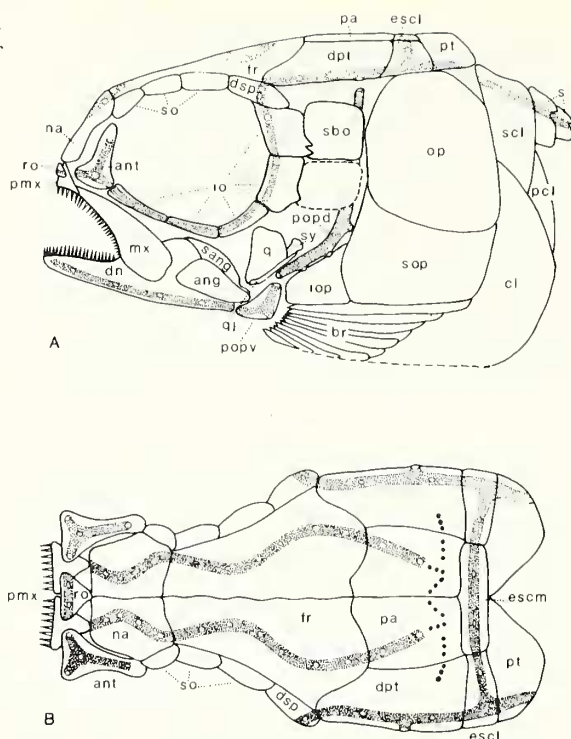

three most dorsal ones follow the usual pattern, with the ventral edge overlapping the preceding ray. This pattern reverses at the fourth ray so that, starting from the fifth, the dorsal margin overlaps the following one. This arrangement is described by Zambelli (1975, 1978, 1981) for all the Norian pholidophorids from Northern Italy.

The dorsal preopercular (text-figs. 2–4) is a very slender bone, gently bent forwards ventrally. Its ventral region is partially exposed and has two or three very short, backwardly-directed pegs, enveloping the branches of the sensory canal. The ventral preopercular lies just behind the lower jaw articulation and in front of the interopercular. It is a small triangular bone bearing the connection between the mandibular and the preopercular sensory canals. A pore is present at the postero-ventral corner of the bone, at the end of a branch leaving the main canal where it bends sharply upwards. A bone in a similar position, also bearing part of the preopercular sensory canal, is present in *Cleithrolepis* and was named quadratojugal by Wade (1935) and Hutchinson (1973). In *Cleithrolepis*, however, the bone is close to the posterior end of the maxilla, which is as long as the lower jaw. Later, Wade (1941) named this bone the 'second preopercular'. Furthermore, Daget (1964) pointed out that the quadratojugal always lies close to the posterior end of the maxilla and in front of the preopercular, having no sensory canal. The quadratojugal (*sensu* Daget 1964) is present in a few actinopterygians (Patterson 1973, p. 249; Gardiner 1984), sometimes bearing traces of the vertical pit-line (*Pteronisculus*, Nielsen 1942; *Canobius ramsayi*, Westoll 1944). Patterson (1973) seems to agree with the interpretation of Daget (1964), not citing *Cleithrolepis* in his list. I also consider this bone as a ventral preopercular, both because of the presence of the sensory canal and its position relative to the very short maxilla. So far, *Prohalecites* is the only fish having a similar bone associated with a short maxilla.

The parasphenoid (text-fig. 5) has a median rounded keel and two lateral wings. Between the keel and each wing there is a groove as in *Hulettia* (Schaeffer and Patterson 1984). The ascending processes arise at the level of the buccohypophysial canal opening, and have a small stout basipterygoid process anteriorly. The posterior portion of the parasphenoid is a flat lamina which is partly seen in only one specimen. No traces of dentition can be seen.

In a few specimens otoliths are visible: in MCSNIO P391/1 (s.l. 24 mm) four otoliths are present just behind the parasphenoid. The anterior two are smaller and may be utricular (lapilli) while the posterior are somewhat bigger and are considered as saccular (sagittae). Otoliths are visible in small specimens; this may simply be due
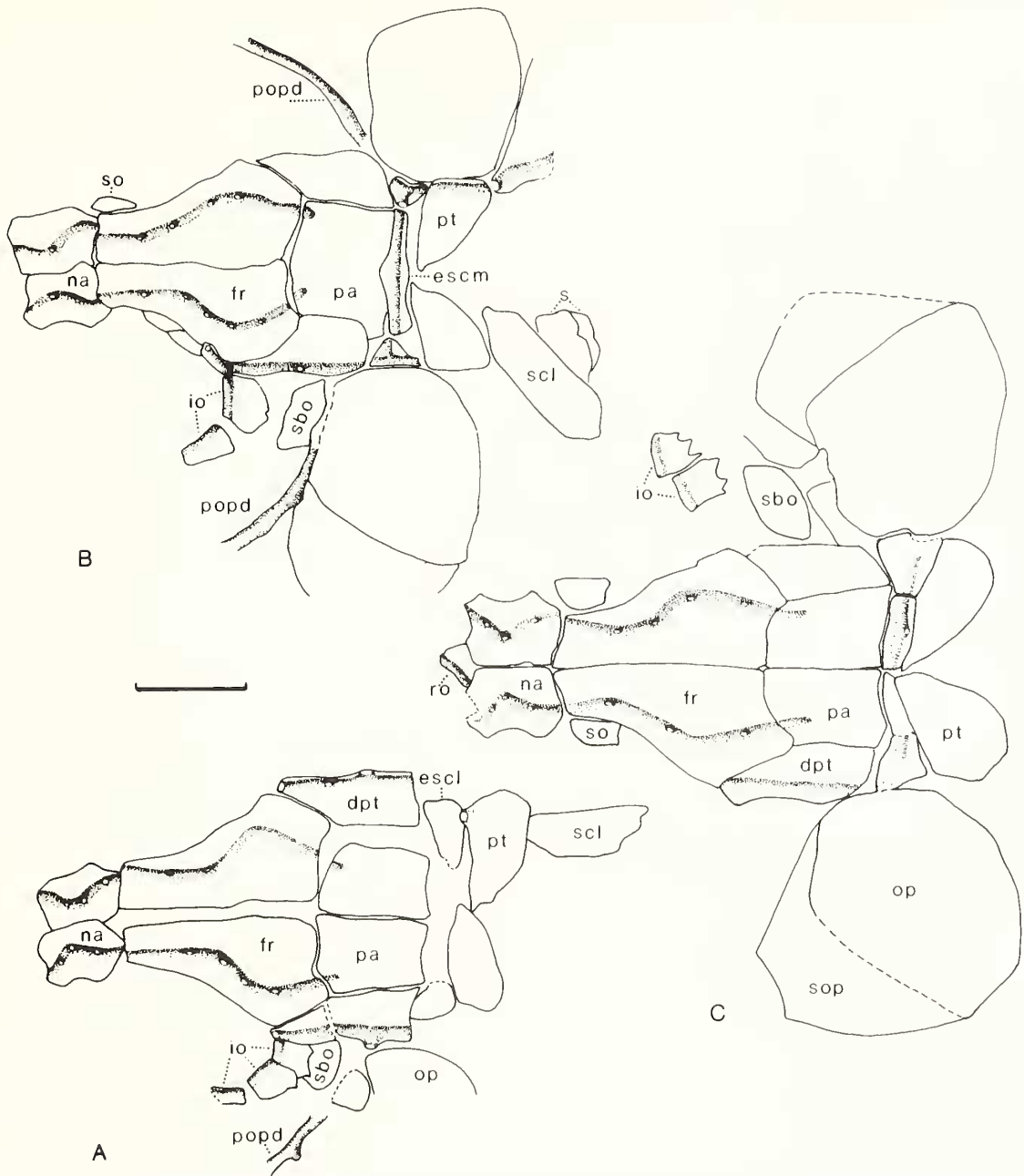
TEXT-FIG. 3. *Prohalecites porroi*. Skull bones as preserved in A, MCSNIO P362, s.l. 35 mm; B, MCSNIO P328/1, s.l. 33 mm (see also text-fig. 1a); C, MCSNIO P377, s.l. 35 mm. Scale bar, 2 mm.

to the thickness of the bones in the juvenile stage: they break up easily above the hard masses of the otoliths themselves.

The hyomandibular (text-figs. 4,5) is large and powerful and perforated by the hyomandibular nerve.

The quadrate (text-figs. 2,4) has a stout articular head, which is buttressed by the anterior end of the quadratojugal (*sensu* Patterson 1973). The quadratojugal is applied to the posterior margin of the quadrate,

TEXT-FIG. 4. *Prohalecites porroi*. Lower jaw and associated preopercular bones as preserved in A, MCSNIO P373/1, s.l. 41 mm (see also pl. 1, fig. 3, text-fig. 7C); B, MCSNIO P373/2, s.l. 37 mm; C, MCSNIO P338, s.l. 33 mm. Scale bars, 2 mm.

TEXT-FIG. 5. *Prohalecites porroi*. Restoration of A, the parasphenoid (dorsal view); B, the hyomandibular (side view).

but it does not fuse to it; the splint-like bone is very similar to that of *Dapedium* and *Lepidotes* (Patterson 1973, p. 293).

The symplectic (text-figs. 2,4) is a triangular bone lying on the inner side between the quadrate and the quadratojugal. It is much larger than the quadratojugal and extends upwards much beyond the quadrate, though not reaching the hyomandibular. So far, no trace of a condyle for articulation with the lower jaw has been detected. However, the proximal tip lies close to the quadrate articular head.

The whole palate is ossified and sutures between the different bones are hard to detect. Some teeth may be present in the anterior region. All the bones, except the quadratojugal, show a cancellous structure.

The ceratohyals are never clearly visible, but possibly there is a small ceratohyal followed by a larger epihyal. The hypohyals are stout and heavily ossified and must have been only weakly tied to each other.

Girdles

In the pectoral girdle the scapulocoracoid is a large plate with a pronounced antero-ventral process. The scapular foramen, close to the antero-dorsal corner, is small and round. On the inner side, a smaller foramen is present ventral to the scapular. In the coracoid region, very close to the posterior margin, there is a large elongated fenestra. At least four elongated, strong pectoral radials are visible which are enlarged distally where they articulate with the lepidotrichia.

The cleithrum (text-fig. 2) is strongly convex and the anterior region is much larger than the posterior one. The external surface shows the same ornamentation as the supracleithrum, i.e. elongated ganoine flecks more or less parallel to the posterior edge.

The supracleithrum (text-figs. 2,3) is narrow and elongated, somewhat wider in the upper region where the sensory canal crossed the whole bone. Posterior to the supracleithrum there are two scales bearing the lateral line. The postcleithrum (text-fig. 2) is elongated dorso-ventrally, with a gently rounded posterior edge. Its outer surface is smooth.
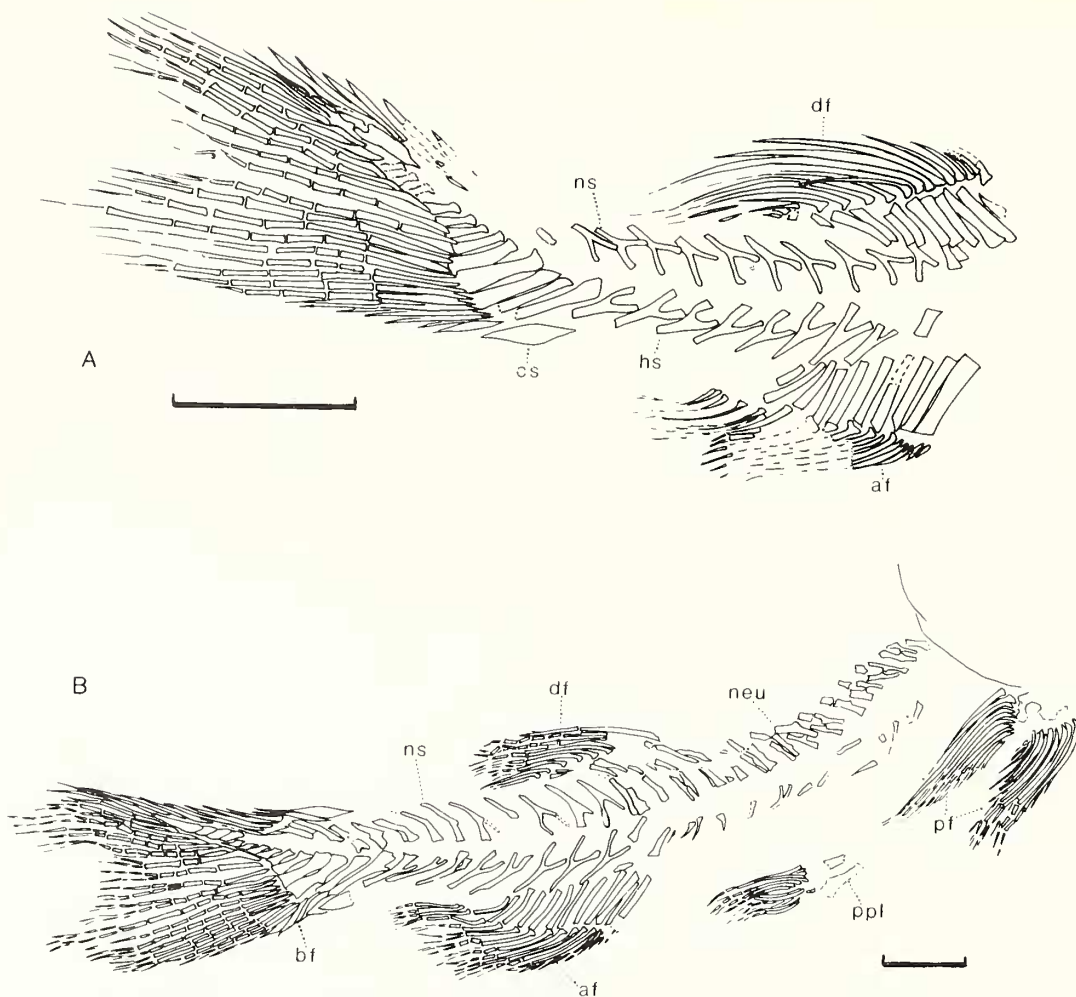
Axial skeleton

The vertebral segments (text-figs. 6–8) number about 33, 20 or 21 of which are in the caudal region. The vertebral centra consist of crescentic hemichordacentra throughout the length of the body. Usually the dorsal and ventral hemicentra do not meet though they are opposite to each other in the caudal region. However, in a couple of specimens a few centra are ring-shaped, showing that fusion has occurred between the two opposing hemicentra.

In the anterior trunk region only dorsal precentra, probably related to cartilaginous intercalaries, and ventral centra with parapophyses, are present. Fully mature specimens show neural arches bearing hemicentra from the 10th–11th vertebral segment. The whole preural part of the caudal region is diplospondylous. Although precentra become larger and larger back to the middle of the caudal region they do not reach the size of centra.

Hemicentra are not present in juvenile specimens: recently Schaeffer and Patterson (1984) described a similar situation for *Hulettia americana* and *Todiltia schoewei*, confirming what Patterson (1973) wrote about *Euricormus*' hemichordacentra. In *Prohalecites*, chordacentra commence in the anterior caudal region in specimens of about 30 mm standard length. Initially, both ventral and dorsal centra appear in that region. Then ventral centra develop anteriorly (but parapophyses are not firmly fixed to them at this stage) and also posteriorly in the ural region. Finally, the dorsal centra reach their full extent and precentra appear. The latter are largest in the mid caudal region. The size of the precentra gives information about two possible growth gradients of the hemichordacentra, as already suggested by Schaeffer and Patterson (1984) for *Hulettia*: backwards in the trunk region and centrifugally from the middle caudal region. That this is the usual pattern is confirmed by observations on Norian Pholidopleuridae now being made by the author.

The neural arches and spines are paired from the first to the 14th–16th segment; then median spines are present. In young individuals, the paired arches and spines are rectangular; in adults they become thinner and more elongated. Supraneurals are present from the first vertebral segment back to the second neural spines beneath the dorsal fin radials. Their proximal ends lie between the distal ends of the paired spines. Paired elongated bean-like bones flank the dorsal tip of the supraneurals, at least in the anterior trunk region. They are in line with the distal parts of the dorsal fin radials (see below). Unfortunately, these bones have been seen only in one of the largest specimen (MCSNIO P413). Similar bones are also known in *Cleithrolepis* (Wade 1935, fig. 25, and p. 54; Patterson pers. comm.), though here they do not have the one-to-one relationship with the supraneurals. Epineurals are well developed as posterolaterally directed outgrowths from the neural arches. They reach their maximum length between the 7th and 10th abdominal neural arches. A small forwardly-directed process is set halfway along the anterior edge of each abdominal neural arch. At the same level, there are rod-like thickenings on the medial surfaces of the arches that may be considered to be supradorsals. These thickenings, and the anterior process, mark the position in life of the longitudinal ligament, as in *Amia* and *Salmo* (Jollie 1973).

Neural and haemal arches become tightly bound to supporting hemicentra in mature specimens. There are large parapophyses beneath the notochord in the abdominal region, which bear long slender pleural ribs. Posterior to the 13th or 14th vertebra there are rather expanded haemal arches, bearing long haemal spines, which are much enlarged in the last three or four pre-ural vertebrae.

TEXT-FIG. 6. *Prohalecites porroi*. Axial skeleton and fins as preserved in A, MCSNIO P400, s.l. 19 mm; and B, MCNSIO P392, s.l. 27 mm. Scale bars, 2 mm.

No intercalaries have been observed except a few paired interventrals in the middle of the caudal region. However, external surfaces of the dorsal precentra are never completely exposed.

Paired fins

The pectoral fins (text-figs. 6–8) are large, their length being usually somewhat less than the head length. Each fin consists of 10 to 12 lepidotrichia preceded by two spines. The leading lepidotrich bears slender fringing fulcra. The proximal segment is very long and the more distal segments somewhat shorter. Each lepidotrich bifurcates only once or twice and always well beyond the commencement of segmentation. The insertion of the pectoral fins is ventral, very close to the mid-line.

The pelvic fins (text-figs. 6–8) are small, with only six to eight long lepidotrichia and two short anterior spines in each. Slender fringing fulcra are present on the leading lepidotrich. The structure of the lepidotrichia is similar to that of the pectoral fin. A pair of long slender bones is the only endoskeletal support of the fins. Each bone has an asymmetrically enlarged distal end.
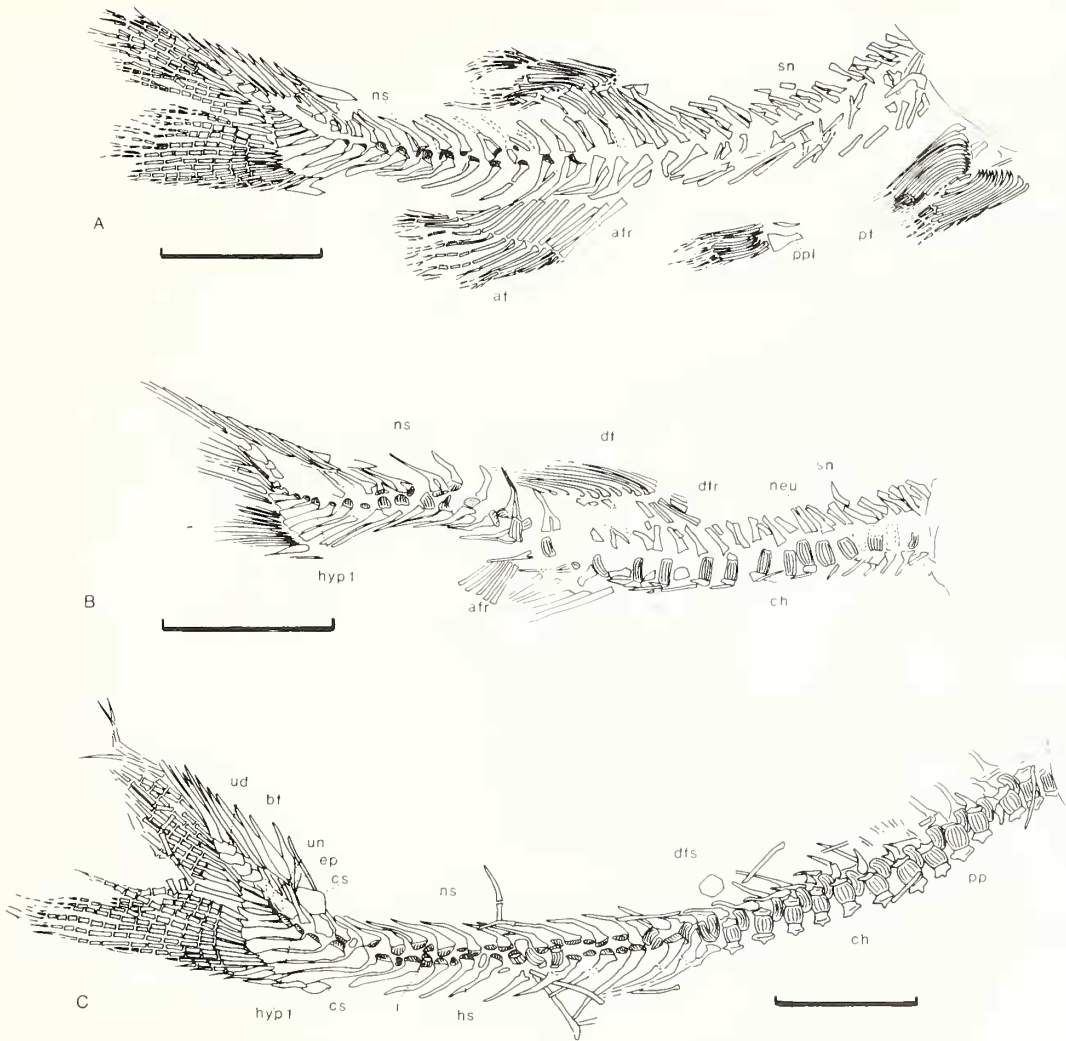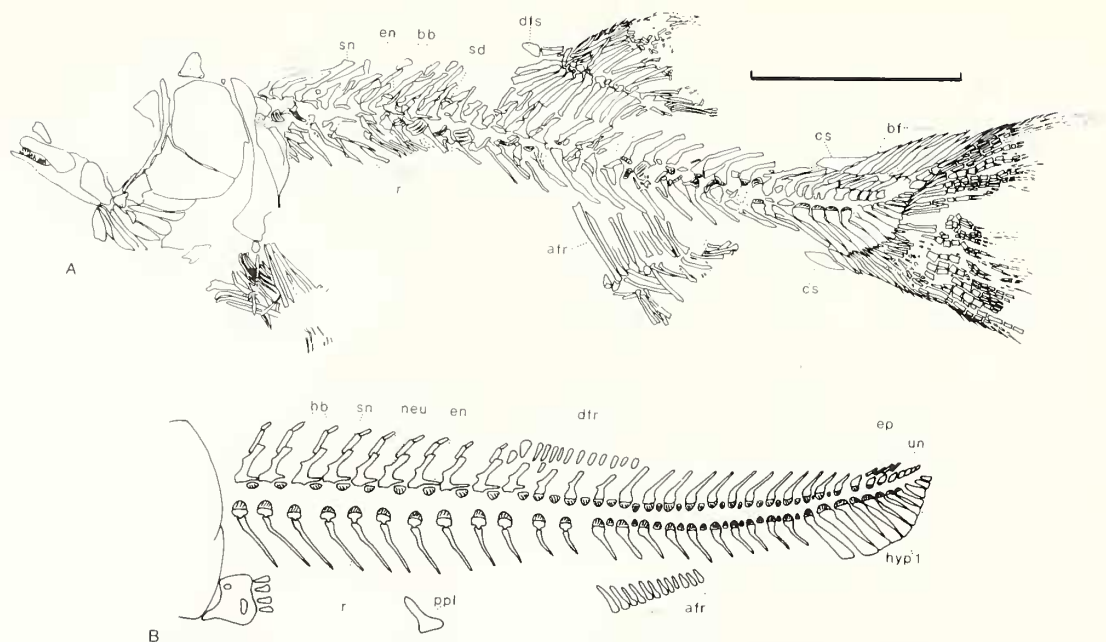
TEXT-FIG. 7. *Prohalecites porroi*. Axial skeleton and fins as preserved in A, MCSNIO P341/1, s.l. 31 mm (see also pl. 1, fig. 4); B, MCSNIO P349a, s.l. 30 mm (see also pl. 1, fig. 2); C, MCSNIO P373/1, s.l. 41 mm. (see also pl. 1, fig. 3, text-fig. 4A). Scale bars, 5 mm.

Unpaired fins

The dorsal fin (text-figs. 6–8) is inserted about half way between the skull roof and the beginning of the caudal fin. The fin is short: 10 to 12 lepidotrichia are preceded by an oval median scale and four or five basal fulcra. The first lepidotrich is unbranched and short, bearing only one or two fringing fulcra. All of the main lepidotrichia branch once; their proximal segment is very long and usually there are two or three more segments before the branching. The general shape of the fin is triangular. The radials are equal in number to the lepidotrichia and the first is much larger than the others and also supports the basal fulcra. Each radial is composed of a long slender proximal part and a couple of very short distal bones which are close to the articulation with the lepidotrichia.

The anal fin (text-figs. 6–8) originates a little more posteriorly than the dorsal. Its shape and size are also comparable, with 12 lepidotrichia, a few basal fulcra and a median scale. Fringing fulcra are borne by the first two lepidotrichia, the second of which is the longest in the fin.
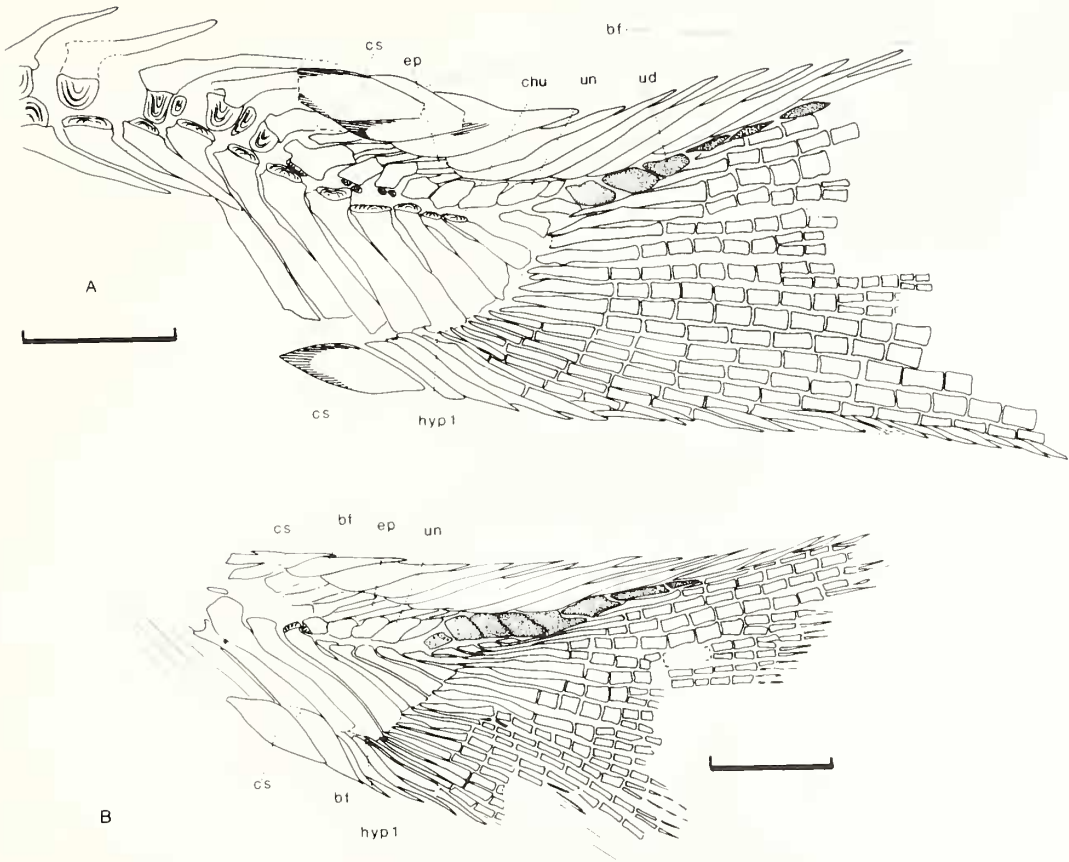
TEXT-FIG. 8. *Prohalecites porroi.* A, MCSNIO P413 as preserved, s.l. 43 mm; scale bar, 10 mm; B, restoration of the axial skeleton.

The caudal skeleton (text-figs. 6–8) is sometimes well exposed but, owing to the small size of the fishes, some structures, such as the ural neural arches, are difficult to interpret.

The striking similarity to the caudal skeleton of the Pholidophoridae (Patterson 1968) helps to determine where the ural structures begin. In a few specimens, a small anterior process is visible at the base of the haemal spine; easier to detect is a change in the anterior outline of the arches from convex to concave or straight. Both these features, together with the upward flexure of the posterior outline of the haemal spines, occur on the fifth elongated haemal spine, which is therefore considered to be the first hypural. The complete hypural series is composed of only six or seven elements. The first two or three, together with the last four haemal spines, support the lower lobe of the fin. The notochord was calcified even in the ural region, but usually only ventral hemicentra are present, as far as the sixth ural centrum. The last dorsal hemicentrum may be the first preural or the first ural. In a couple of specimens two hypurals are borne by a single hemicentrum, much larger than the others: the first and the second urals in one specimen, the second and the third in the other. In at least one of these specimens there is one more double hemicentrum in the caudal region but in a dorsal position; it bears two pairs of neural arches which are fused into a single median neural spine. Furthermore, in this specimen, a ring-shaped centrum is found in the middle of the caudal region. In the light of these facts the occasional fusion of the ural ventral hemicentra is considered an individual malformation rather than an indication of relationship (Patterson 1973; Schaeffer and Patterson 1984).

Again, as in the Pholidophoridae s.s., the last three preural neural spines, which remain unpaired, gradually decrease in length. Posterior to them there are three or four long epurals. There are six or seven ural neural arches in one-to-one correspondence with the hypurals. They are always preserved in lateral view so that it is impossible to determine whether or not they lack a median spine. The first two or three are rather similar to each other and, though smaller, do not differ in shape from the last preural neural arches. The more posterior ural neural arches are small, longitudinally elongated and close to each other, giving rise to a continuous cover over the neural canal and approaching or even touching the hypural bases. Though similar to those of pholidophorids in their general aspect, these ural neural arches are surely more primitive. *Dapedium* too has similar structures, but its preural neural arches are paired (Patterson 1973). On the other hand, the modified arches are hollowed anteriorly to receive the posterior edge of the preceding arch, as illustrated in *Pholidophorus bechei* by Patterson (1968), and they also closely resemble the last three ural neural arches in

TEXT-FIG. 9. *Prohalecites porroi*. Caudal fin as preserved in A, MCSNIO P331, s.l. unknown; B, MCSNIO P335, s.l. 30 mm (see also text-fig. 1E). Urodermal shaded. Scale bars, 2 mm.

Leptolepis coryphaenoides (Patterson 1968). I therefore consider these ural neural arches to be uroneurals, comparable to those of *Dapedium* and of the Pholidophoridae s.s. (Patterson 1968, 1973).

The caudal fin is moderately forked and almost symmetrical in its outline. There are 14 to 18 principal lepidotrichia, seven or eight in the lower lobe and seven to ten in the upper. The lowermost and perhaps the uppermost two principal lepidotrichia are unbranched; all the others branch once or twice. In the lower lobe, the leading ray bears fringing fulcra in its distal part, and is preceded by three or four unbranched but segmented shorter rays, which also bear a few fringing fulcra. Usually, four basal fulcra are present; they are preceded by a median scale with a short anterior process. This latter scale is considered to be a caudal scute. In the upper lobe, the proximal ends of the lepidotrichia become more and more asymmetrical upward, so that long, downwardly bent processes overlap the complete series of the upper hypurals. Along the upper margin of the fin there is a caudal scute, larger than the ventral one, and ten basal fulcra followed by slender fringing fulcra on the uppermost lepidotrich. The anterior tips of the basal fulcra lack ganoine, but the remainder of their surface is enamelled, even where covered by the preceding fulcrum.

Squamation

Most of the body of *Prohalecites* was naked or covered by very thin scales which have left no trace. In several specimens, however, the body outline is shown by small carbonized patches, much closer to each other in the abdominal region. The only known scales are ganoine-covered; for example, the two at the beginning of the lateral line just posterior to the supracleithrum, or the median ones in front of the unpaired fins. At the base

of the upper lobe of the tail there is an elongated patch of eight to ten scales, arranged in a long row of six to eight scales with one or two more rounded ones dorsally. They are clearly homologous to the urodermals of some pholidophorids (Patterson 1968). The scales of the main row show more or less the same shape as the posterior uroneurals, but each slightly overlaps the following one. The two upper urodermals are overlapped by the epaxial basal fulcra. The whole urodermal scale patch covers the proximal ends of the upper lobe lepidotrichia, but seems to lie just posterior to the last uroneural and hypural; thus the uroneurals form a continuous series with the urodermals, except that the two are distinguished by the marginal overlapping of the urodermals.

TAXONOMIC REMARKS

Relationships of Prohalecites

No detailed anatomical description of *Prohalecites* has been made since that of De Alessandri (1910), but the genus was often mentioned or listed in papers concerning Triassic fish faunas. Brough (1939, p. 107) considered *Prohalecites* as a possible sub-holostean while both Griffith (1977, p. 81) and Patterson (1981, p. 217) tentatively ascribed the genus to primitive teleosts, perhaps in the light of its original designation as '*Pholidophorus*'.

Even now, after a much more detailed description, the taxonomic position of *Prohalecites* is difficult to define owing to the presence of both advanced and primitive characters. In many respects (especially the axial skeleton), it seems to fit rather well in the Pholidophoridae s.s.

Outside the Pholidophoridae, chordacentra are known in the Pholidopleuridae and Caturidae (Patterson 1973), Ophiopsidae (Bartram 1975), *Hulettia*, and immature *Todiltia* (Schaeffer and Patterson 1984), as well as in several other groups. Furthermore, they seem to be present also in other undescribed genera from the Italian Upper Triassic (pers. obs.).

The caudal endoskeleton shows more or less the same organization as in pholidophorids, with ural neural arches slightly modified and approaching the uroneural stage. The dermal skull also shows a striking resemblance to the pholidophorids in the position and shape of the quadratojugal, even though this bone is not yet fused with the quadrate in *Prohalecites*. The infraorbitals are also very similar in shape apart from the postero-ventral one. Many other characters, however, are remarkably different: for example the snout pattern has large contiguous nasals, the preopercular is double and shows a tube-like dorsal part, the maxilla is very short, and there are no supramaxillae. Thus, *Prohalecites* cannot be placed in the Pholidophoridae *sensu* Nybelin (1966), or even as emended by Zambelli (1981), or *sensu* Patterson (1973).

The dermal skull pattern of *Prohalecites* is much like that of advanced Parasemionotidae (*sensu* Patterson 1973), genera such as *Promecosomina* and especially *Paracentrophorus* and *Phaidrosoma* (Griffith 1977), but Parasemionotidae have no vertebral centra (Patterson 1973), while *Paracentrophorus* has no fringing fulcra (Gardiner 1960). *Prohalecites* also shows some resemblance to the Caturidae, but their quadrate and symplectic articulation with the lower jaw is so far unknown in *Prohalecites*.

The very short maxilla, without any supramaxilla, is here considered a derived character which might have formed either by the shortening of a long toothed maxilla and the concomitant loss of the supramaxilla, or directly from a maxilla not yet provided with a supramaxilla. This opinion is in contrast with that of Schaeffer and Patterson (1984) who consider the lack of supramaxillae as a primitive character in *Hulettia*, as in all the other chondrosteans with long maxillae. In some Parasemionotidae, *Promecosomina* and *Phaidrosoma* for instance, the supramaxilla is also absent and the maxilla is rather short.

Among Triassic fishes, the Semionotidae with grinding dentition also show a short maxilla, but this is usually toothless. The caudal endoskeleton of *Prohalecites* is rather similar to that of *Dapedium* (Patterson 1973, fig. 27), which is, in my opinion, close to *Pholidophorus bechei* (Patterson 1968, fig. 5). In many other respects, apart from the large contiguous nasals in *Dapedium* and some other genera, the narrow but single opercular and the splint-like quadratojugal in *Lepidotes* and *Dapedium* (Patterson 1973), the Semionotidae are quite different from *Prohalecites*. The heavy scale covering, lack of chordacentra (but *Tetragonolepis* apparently does have them; Patterson 1973,

p. 294), small mouth, and body more or less elevated are in contrast with the characters of *Prohalecites*.

Since no trace of scales is preserved in any specimen, the body of *Prohalecites* is considered naked. This helps little in the search for possible relatives; among the inferred ancestors, none shows thin or absent scales, but scales are wanting in a few Pholidophoridae and Caturidae. This lack of a scale covering led Woodward (1895) to consider *Prohalecites porroi* all as immature specimens. However, De Alessandri (1910) pointed out that, though the smallest specimens may well be young, the large ones show adult characters, especially in body proportions. Though De Alessandri's arguments are perhaps superficial, the ontogenetic development of the vertebral column described herein proves without doubt that *Prohalecites porroi* represents a naked species of about 40 mm standard length. Moreover, fishes other than *Prohalecites* are uncommon in the Ca' del Frate beds, comprising less that 10% of the total collected specimens from about ten other species. None of the latter shows any tendency towards a reduction in scale covering.

Less important characters, such as fusion of the parietals and the presence of a median extrascapular, are found in *Amia*, *Sinamia*, and *Ikechaoamia* (Patterson 1973; Stensio 1935; Su Te-tsao 1973; Zhang Mi-man and Zhang Hong 1980; Jain 1985). However, this character alone is not sufficient to prove a relationship, because fusion of the parietals has occurred several times in different groups, including the Pholidophoridae themselves (Zambelli 1975, 1978), while a median extrascapular is common in many stem-group neopterygians.

In *Prohalecites*, a ventral preopercular separates the interopercular from the hind edge of the lower jaw as in Macrosemiidae. This was considered a unique specialization of that family by Bartram (1977). Apart from this last character, and the partial fusion between the quadratojugal and quadrate, macrosemiids and *Prohalecites* are very different in other features.

Recently, Schaeffer and Patterson (1984) gave a detailed description of *Hulettia americana*, a mid-Jurassic fish, which is rather similar to *Prohalecites* in many features. Major differences between the two genera are the position of the rostral, which is anterior to the totally contiguous nasals in *Prohalecites*, and the caudal endoskeleton. In this latter, *Prohalecites* shows hemichordacentra and ossified ural neural arches, which can be considered as uroneurals *sensu* Patterson (1973); none of these characters is present in *Hulettia*.

The fact that *Prohalecites* is a neopterygian is proved by the presence of several characters among those listed by Patterson (1973), such as the reduced body lobe of the tail, dorsal and anal fin radials equal in number to their lepidotrichia, premaxilla with nasal process, coronoid process of the lower jaw, suspensorium vertical, tube-like dorsal preopercular and loss of clavicles. However, problems arise when trying to evaluate closer relationships. Similarities between *Prohalecites* and the Parasemionotidae and Caturidae for example are not substantiated and there is no articulation between the symplectic and the lower jaw in *Prohalecites* itself. This articulation, however, is also not recorded in Parasemionotidae s.l. such as *Paracentrophorus*, *Promecosomina*, and *Phaidrosoma* which are the closest to *Prohalecites* at least in the skull-bone pattern. On the other hand, the presence of chordacentra in *Prohalecites* makes it difficult to put all these genera together.

What relationships exist with the Pholidophoridae is difficult to determine: very close similarities are seen in the caudal endoskeleton and in a few characters of the dermal skull. That the quadratojugal is not completely fused with the quadrate is primitive with respect to the pholidophorids, but the juxtaposition of these elements is similar. Unfortunately, there is a lack of neurocranial information for *Prohalecites*.

It is also worth considering the similarities between *Prohalecites* and *Dapedium*. Once more, the caudal skeleton as well the lower jaw joint are very similar in the two. On the other hand, the similarities of *Prohalecites* both with *Dapedium* and with the Pholidophoridae is consistent with Olsen's (1984) view that *Dapedium* was the closest relative of *Pholidophorus*.

In conclusion, *Prohalecites* is clearly more advanced than the Parasemionotidae and somewhat more primitive than *Dapedium* and the Pholidophoridae; moreover, it is certainly closer to the last two than to the former. Nevertheless, I think it better to leave *Prohalecites* as a Neopterygian *incertae sedis* because its characters do not perfectly fit in any of these cited groups.

Species of Prohalecites

Other problems arise at the species level because of the different preservation of the Perledo and Ca' del Frate specimens. A comparison between the two groups of specimens show that they are very similar in most of the known characters. According to De Alessandri (1910) the standard length range is 20–45 mm, comparable with the 19–43 mm range of my specimens. Fin positions and lepidotrichia number are also similar in each, except for the caudal fin. In the latter, De Alessandri recorded 25–26 segmented rays with six more 'anterior rays, small and shortening backwards'. Four of the Ladinian specimens (SM p1247, 54, 62 and MPUN M174), however, show a smaller caudal fin with less than 20 principal rays, as in the Ca' del Frate specimens; the others are too poorly preserved to count the lepidotrichia. Hemichordacentra are found in both groups, ranging in number from 32 (De Alessandri 1910) to 33–35 in the Ca' del Frate specimens. The scales also have the same distribution, few in number and only at the base of the upper lobe of the caudal fin.

The two most remarkable differences are the opercular shape, triangular in the Ladinian specimens (De Alessandri 1910) but rectangular in the Carnian, and the absence of teeth in the Ladinian specimens (De Alessandri 1910) compared with the well-toothed mouth of the new specimens. However, I have been able to prepare specimen MPUN M173, the only Perledo one with bone preserved: teeth are present at least on the lower jaw. Considering that two of the supposed differences resulting from De Alessandri's description proved to be untrue, we may have doubts regarding the other character. The Perledo specimens can easily be misinterpreted owing to their poor preservation.

On the basis of these considerations I include the new Carnian material in the existing *Prohalecites* species, *P. porroi* (Bellotti 1857), at least until new or better preserved material from Perledo, or from coeval beds, is found.

So far, *P. porroi* is still the only species of *Prohalecites* because '*Pholidophorus*' *microlepidotus* Kner 1866 is very different: it has cycloid scales, a large caudal fin with about 40 lepidotrichia, including few epaxial rays, no vertebral centra, and no pelvic fins (pers. obs.). Therefore, it cannot be related to *Prohalecites porroi*, even if Kner (1866) himself thought the two species very close to each other. On the other hand, Deecke (1889), in proposing the new genus *Prohalecites* for *Pholidophorus porroi*, also noticed some differences, which suggested that Kner's species should not be included.

GENERAL REMARKS

Nybelin (1966, 1974) placed great emphasis on the preopercular structure in establishing phylogenetic relationships, and subsequently the reduction of the dorsal limb of the preopercular has been used for hypothesizing relationships between *Amia*, gars, and teleosts (Olsen 1984).

The preopercular in the most advanced Parasemionotidae (*sensu* Patterson 1973), such as *Paracentrophorus*, *Promecosomina*, and *Phaidrosoma*, is very narrow, much like the dorsal preopercular in *Prohalecites*, but with no posterior branches of the sensory canal (Gardiner 1960). Lehman (1952) and Lehman *et al.* (1959) postulated that this narrow preopercular might well have been produced in some Paraseminotidae (*Thomasinotus*, *Stensionotus*, and *Jacobuhis*) by separation of the suborbitals (fragmentation), thus losing the area in front of the sensory canal. A few very short branches of the sensory canal are found in *Prohalecites*, while in the Pholidophoridae they are longer and surrounded by laminar bone, and the posterior region is expanded. The ventral preopercular of *Prohalecites* has one long branch of the sensory canal, but it is expanded posteriorly so that it could bear additional branches.

In *Leptolepis normandica* (Nybelin 1974), as well as in some Recent teleosts such as the salmon, the preopercular comprises two bones; a ventral compound one, with canal elements attached to a laminar base early in ontogeny, and a small dorsal tubular bone called the suprapreopercle (Jollie 1984). The dorsal preopercular of *Prohalecites* is not strictly homologous to the suprapreopercle, since it is usually associated with three or four neuromasts, whereas the suprapreopercle has none (Jollie 1984). However, both the dorsal preopercular and the suprapreopercle are simple canal
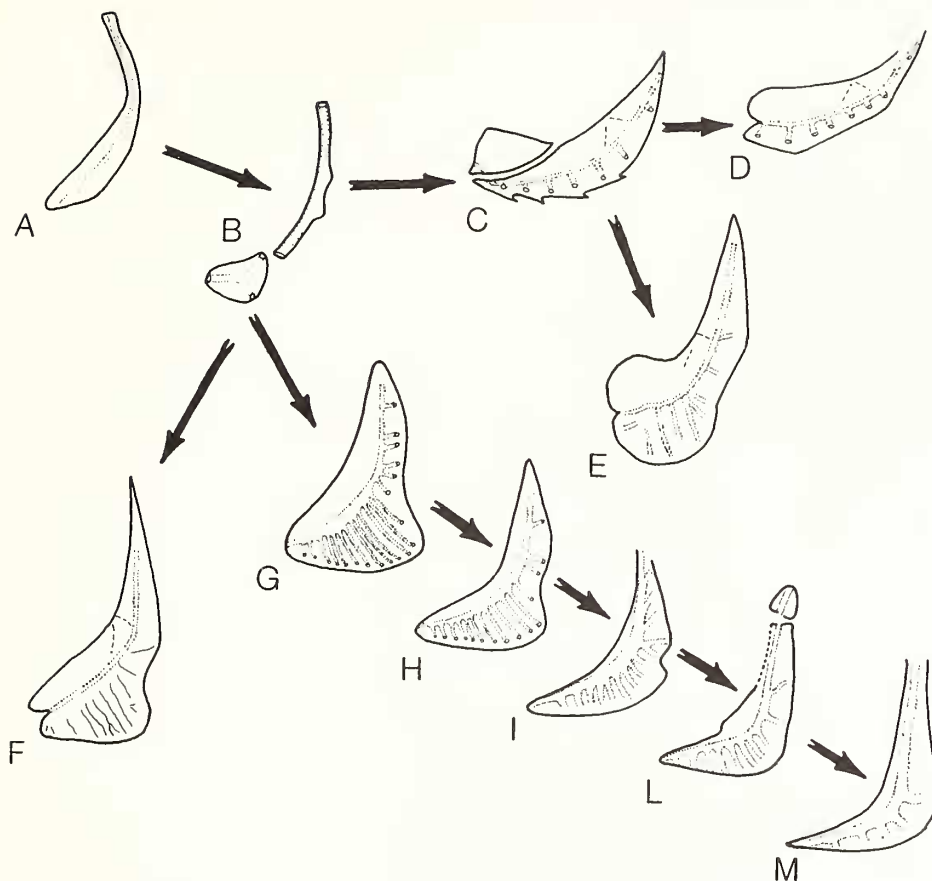
TEXT-FIG. 10. Possible evolution of the preopercular bone(s). A, *Phaidrosoma hunzensis*, after Griffith 1977, fig. 23; B, *Prohalecites porroi*; C, *Pholidoctenus serianus*, after Zambelli 1978, fig. 1; D, *Parapholidophorus nybelini*, after Zambelli 1975, fig. 1; E, *Pholidorhynchodon malzannii*, after Zambelli 1980, fig. 1; F, *Pholidophorus latiusculus gervasuttii*, after Zambelli 1980, fig. 1; G, *Pholidophorus bechei*, after Nybelin 1966, fig. 16; H, *Pholidolepis dorsetensis*, after Nybelin 1966, fig. 16; I, *Proleptolepis furcata*, after Nybelin 1974, fig. 17k; L, *Leptolepis normandica*, after Nybelin 1974, fig. 2e; M, *Leptolepides sprattiformis*, after Nybelin 1974, fig. 30a.

bones. This may be interpreted as a tendency in neopterygians to have more than one bone along the preopercular sensory canal, but with only the ventral part as a compound (tubular plus laminar) bone.

The *Prohalecites* ventral preopercular resembles in shape the ventral region of the preopercular in a few pholidophorids, such as *Pholidophorus latiusculus*, *P. bechei*, and *Pholidolepis dorsetensis* (Nybelin 1966, p. 428), and *Pholidorhynchodon malzannii* (Zambelli 1981). Furthermore, in another pholidophorid, *Pholidoctenus serianus* (Zambelli 1978), the preopercular is double, its antero-ventral part bearing only a very short sensory canal. Zambelli (1978) noted that the two preopercular bones in *Pholidoctenus* are very similar in shape to the single preopercular of other Triassic pholidophorids, implying that the genus was derived from genera more advanced in other characters by splitting of the preopercular. Zambelli (1986) wrote that the anterior preopercular of *Pholidoctenus* was lost in the main pholidophorid lineage during the Jurassic, leaving the quadrate uncovered by dermal bone. In my opinion, this is incorrect, because in other pholidophorid genera the sensory canal ran ventral to the notch which Zambelli (1978, fig. 4) interpreted as the point of separation of the parts of the preopercular. Since, in Parasemionotidae, the preopercular is

presumed to have lost the sensory canal-free anterior region, it seems improbable that part of the sensory canal itself appeared again on a suborbital-like bone. I think that *Pholidoctenus* (which is a primitive genus because its nasals are contiguous for their whole length) could more easily have achieved its preopercular structure by ventral growth of the principal bone, while the primitively separate ventral bone shifts forward, losing most of its sensory canal. A further step was the fusion of the two bones (as is presumed to have occurred in the other Triassic genera) resulting in the absence of the sensory canal in the area anterior to the antero-ventral notch. The groove on the inner surface, starting from this notch, is here interpreted as a trace of fusion and not as an early stage of splitting (Zambelli 1978, 1986). Accordingly, I think that Nybelin's assumption (1966, p. 429) about the primitiveness of the preopercular sensory canal position on the bone is incorrect.

In more advanced Parasemionotidae, the narrow stage of the preopercular had already been reached, and in *Prohalecites*, as we have seen, it is just a tube of bone round the sensory canal. Acquisition of the inflated postero-ventral region, together with the long posterior branches of the sensory canal, could be achieved by the formation of a ventral preopercular as in *Prohalecites* and the subsequent fusion of these two preopercular bones. This fusion may have occurred more than once, giving two distinct patterns. The first is seen in *Pholidoctenus* and most of the other Triassic pholidophorids (text-fig. 10C, D, E) where the ventral preopercular is presumed to have fused along the antero-ventral edge of the dorsal preopercular.

The second pattern is thought to have developed from a more simple dorso-ventral fusion between the two bones, which often leaves a posterior notch, as in *Pholidophorus latiusculus* (text-fig. 10F) and a few Jurassic pholidophorids (*Pholidophorus bechei* and *Pholidolepis dorsetensis* as well as in *Proleptolepis* for instance; text-fig. 10G, H, I). If *Prohalecites* was ancestral to the Pholidophoridae, then a preopercular such as that of *Pholidoctenus* is primitive compared to that of the other late Triassic pholidophorids (with a deep antero-ventral notch), and *Pholidoctenus* and *Pholidorhynchodon* could not have been ancestral to the main Lower Lias pholidophorid to leptolepid lineage. Nybelin had already noticed this fact (1966, fig. 16) that all the Lias species are derived from unknown or hypothetical ancestral forms.

Recently, Zambelli (1986) also wrote that no Upper Triassic genus of his new subfamily Pholidophorinae (*Pholidophorus*, *Parapholidophorus*, *Pholidoctenus*, and *Pholidorhynchodon*) could be directly ancestral to teleosts, even if he supposed that *Pholidophorus* had to be the closest relative to Lias Pholidophoridae.

Finally, concerning the shape of the preopercular, *Amia* is like the Parasemionotidae, while gars, in which the ventral branch is well developed and L-shaped, are most like the leptolepids. If relationships between *Prohalecites* and the pholidophorids are to be strengthened, then this preopercular character could be of interest in relation to the different hypotheses (Patterson 1973; Olsen 1984) for gars, *Amia* and teleost relationships.

Abbreviations

af, anal fin; afr, anal fin radial; ang, angular; ant, antorbital; asp, ascending process of parasphenoid; bb, 'bean' bone; bf, basal fulcra; bp, basipterygoid process of parasphenoid; br, branchiostegal ray; ch, hemichordacentrum; chu, ural hemichordacentrum; cl, cleithrum; cs, caudal scute; df, dorsal fin; dfr, dorsal fin radial; dfs, dorsal fin scale; dn, dentary; dpt, dermopterotic; dsp, dermosphenotic; en, epineurals; ep,

epurals; escl, lateral extrascapular; escm, median extrascapular; fr, frontal; hs, haemal spine; hym, hyomandibular; hypl, first hypural; i, intercalary; io, infraorbital; iop, interopercular; lw, lateral wing of parasphenoid; mx, maxilla; na, nasal; neu, paired neural arch and spine; ns, median neural spine; op, opercular; opr, opercular process of hyomandibular; pa, parietal; pf, pectoral fin; pcl, postcleithrum; pmx, premaxilla; popd, dorsal preopercular; popv, ventral preopercular; pp, parapophysis; ppl, pelvic plate; pt, posttemporal; q, quadrate; qj, quadratojugal; r, pleural ribs; ro, rostral; s, lateral line scale; sang, surangular; sbo, suborbital; scl, supracleithrum; sd, supradorsal; sn, supraneural; so, supraorbital; sop, subopercular; sy, symplectic; ud, urodermal; un, uroneural.

REFERENCES

BARTRAM, A. W. H. 1975. The holostean fish genus *Ophiopsis* Agassiz. *Zoological Journal of the Linnean Society* **56,** 183–205.

—— 1977. The Macrosemiidae, a Mesozoic family of holostean fishes. *Bulletin of the British Museum (Natural History), Geology Series,* **29,** 127–234

BELLOTTI, C. 1857. Descrizione di alcune nuove specie di pesci fossili di Perledo e di altre localitá lombarde. 419–432. *In* STOPANI, A. (ed.). *Studi geologici sulla Lombardia.* Editore Turati, Milano

BROUGH, J. 1939. *The Triassic fishes of Besano, Lombardy.* British Museum (Natural History), London, 117 pp.

COSTA, G. O. 1853–1860. *Ittiologia fossile italiana.* Napoli, 67 pp.

DAJET, J. 1964. Le crânc des téléostéens. *Mémoires du Museum nationale d'Histoire naturelle,* A **32,** 163–342.

DE ALESSANDRI, G. 1910. Studi sui pesci triassici della Lombardia. *Memorie della Societa Italiana di Scienze Naturali,* **3,** 1–145.

DEECKE W. 1889. Ueber Fischer aus vershiedenen Horizonten der Trias. *Palaeontographica,* **35,** 97–138.

GARDINER, B. G. 1960. A revision of certain actinopterygian and coelacanth fishes, chiefly from the Lower Lias. *Bulletin of the British Museum (Natural History), Geology Series,* **4,** 241–384.

—— 1984. The relationships of the palaeoniscid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia. *Bulletin of the British Museum (Natural history), Geology Series,* **37,** 173–428.

GRIFFITH, J. 1977. The Upper Triassic fishes from Polzberg bei Lunz, Austria. *Zoological Journal of the Linnean Society,* **60,** 1–93.

HUTCHINSON, P. 1973. A revision of the redfieldiiform and perleidiform fishcs from the Triassic of Bekker's Kraal (S. Africa) and Brookvale (New South Wales). *Bulletin of the British Museum (Natural History), Geology Series,* **22,** 233–254.

JAIN, S. L. 1985. Variability of dermal bones and other parameters in the skull of *Amia calva. Zoological Journal of the Linnean Society,* **84,** 385–395.

JOLLIE, M. 1973. *Chordate morphology.* R. E. Krieger, Huntington, 478 pp.

—— 1984. Development of the head skeleton and pectoral girdle of salmons, with a note on the scales. *Canadian Journal of Zoology,* **62,** 1757–1778.

KNER, R. 1866. Die Fische der bituminosen Schiefer von Raibl in Karnthen. *Sitzungsberichte der Akademie der Wissenschaften in Wien,* **53,** 152–197.

LEHMAN, J. P. 1952. Étude complémentaire des poissons de l'Eotrias de Madagascar. *Kongliga svenska vetenskapsakademies Handlingar,* **2,** 1–202.

—— CHATEAU, C., LAURAIN, M. and NAUCHE, M. 1959. Paléontologie de Madagascar. XXVIII. Les poissons de la Sakamena moyenne. *Annales de paléontologie,* **45,** 175–219.

NIELSEN, E. 1942. Studies on Triassic fishes from East Greenland. I. *Glaucolepis* and *Boreosomus. Meddelelser om Gronland,* **138,** 1–394.

NYBELIN, O. 1963. Zur Morphologie und Terminologie des Schwanzskelettes der Actinopterygier. *Arkiv for Zoologi,* **15,** 485–516.

—— 1966. On certain Triassic and Liassic representatives of the family Pholidophoridae s. str. *Bulletin of the British Museum (Natural History), Geology Series,* **11,** 353–432.

—— 1974. A revision of the leptolepid fishes. *Acta Regiae Societatis scientiarum et litterarum gothoburgensis (Zoologica),* **9,** 1–202.

OLSEN, P. R. 1984. The skull and pectoral girdle of the parasemionotid fish *Watsonulus eugnathoides* from the Early Triassic Sakamena Group of Madagascar, with comments on the relationships of the holostean fishes. *Journal of Vertebrate Paleontology,* **4,** 481–499.

PATTERSON, C. 1968. The caudal skeleton in Lower Liassic pholidophorid fishes. *Bulletin of the British Museum (Natural History), Geology Series,* **16,** 203–239.

—— 1973. Interrelationships of holosteans. 233–305. In GREENWOOD, P. H., MILES, R. S. & PATTERSON, C. (eds), *Interrelationships of fishes*, Academic Press, London.

—— 1981. Agassiz, Darwin, Huxley, and the fossil record of teleost fishes. *Bulletin of the British Museum (Natural History), Geology Series*, **35**, 213–224.

SCHAEFFER, B. and PATTERSON, C. 1984. Jurassic fishes from the Western United States, with comments on Jurassic fish distribution. *American Museum Novitates*, **2796**, 1–86.

STENSIÖ, E. A. 1935. *Sinamia zdanskyi*, a new amiid from the Lower Cretaceous of Shantung, China. *Paleontologia Sinica*, C3, 1–48.

SU TE-TSAO 1973. A new *Sinamia* (*S. huananensis*, sp. nov.) from the Upper Jurassic of Southern Anhui. *Vertebrata Palasiatica*, **11**, 149–153.

TINTORI, A. and RENESTO, S. 1983. The Macrosemiidae (Pisces, Actinopterygii) from the Upper Triassic of Lombardy (N. Italy). *Rivista italiana di Paleontologia e Stratigrafia*, **89**, 209–222.

—— MUSCIO, G. and NARDON, S. 1985. The Triassic fossil fishes localities in Italy. *Rivista italiana di Paleontologia e Stratigrafia*, **91**, 197–210.

WADE, R. T. 1935. *The Triassic Fishes of Brookvale, New South Wales*. British Museum (Natural History), London, 110 pp.

—— 1941. Australian Triassic Fishes. I. The Triassic fishes of St. Peter's, Sydney, New South Wales. II. The relationships of the Australian Triassic fishes to each other and to other bony fishes. *Journal and Proceedings of the Royal Society of New South Wales*, **74**, 377–396.

WESTOLL, T. S. 1944. The Haplolepidae, a new family of Late Carboniferous bony fishes. *Bulletin of the American Museum of Natural History*, **83**, 1–121.

WOODWARD, A. S. 1895. *Catalogue of the fossil fishes in the British Museum (Natural History)*. British Museum (Natural History), London, 544 pp.

ZAMBELLI, R. 1975. Note sui Pholidophoriformes. I. *Parapholidophorus nybelini* gen. n. sp. n. *Istituto Lombardo Accademia di Scienze e Lettere*, B109, 3–49.

—— 1978. Note sui Pholidophoriformes. II. *Pholidoctenus serianus* gen. n. sp. n. *Rendiconti Accademia Nazionale delle Scienze detta Dei*, **XL**, **3**, 101–124.

—— 1981. Note sui Pholidophoriformes. IV. contributo: *Pholidorhynchodon malzannii* gen. n. sp. n. *Rivista Museo civico Scienze naturali " E. Caffi "*, **2 (1980)**, 129–159.

——1986. note sui Pholidophoriformes. VI. contributo: Pholidophorinae subfamiglia nuova del Triassico Superiore. *Rivista Museo civico Scienze naturali " E. Caffi "*, **10**, 1–32.

ZHANG MI-MAN & ZHANG HONG 1980. Discovery of *Ikechaoamia* from South China. *Vertebrata Palasiatica*, **18**, 89–93.

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